PAN-PACIFIC ENTOMOLOGIST
72(2): 70–81, (1996)

# THE NATURAL HISTORY OF *NICROPHORUS NIGRITA*, A WESTERN NEARCTIC SPECIES (COLEOPTERA: SILPHIDAE)

Derek S. Sikes[1]
Department of Biology, University of California,
Santa Cruz, California 95064

*Abstract.*—*Nicrophorus nigrita* Mannerheim is an atypical Nearctic burying beetle due to its lack of dorsal, elytral maculations. Aspects of this species' natural history were investigated and compared to those of Nearctic congeners. Adults from a central Californian coastal population were found to be crepuscular and active year-round, with minimal activity during winter. The sex ratio of wild-trapped *N. nigrita* was female-biased while laboratory-raised broods were slightly male-biased. Adult male pronotal width was greater than that of females (mean ± SD) (5.84 ± 0.74 vs. 5.67 ± 0.66). A minimum population size of 4565 individuals was calculated for Big Creek Canyon. Analysis of mouse carcass transect data indicated that *N. nigrita* adults located dead mice more successfully in moist, cool, redwood-forested canyons than in six other habitat-types. Vertebrate scavengers, flies and ants were the most common competitors of *N. nigrita* for mouse carcasses. The reproductive biology of this species differed only slightly from known *Nicrophorus* biology. Carcass mass strongly predicted the mean pronotal width of the offspring in a brood. *Nicrophorus nigrita* differs from Nearctic congeners in the lack of elytral maculations, the greater length of time required to complete development from larva to adult and an apparent lack of reproductive diapause. It only shares year-round activity with *Nicrophorus mexicanus* Matthews.

*Key Words.*—Insecta, *Nicrophorus nigrita*, Silphidae, Nicrophorinae, burying beetle, carrion, Acari, Parasitidae, *Poecilochirus carabi*, *P. subterraneus*, Histiostomatidae, *Pelzneria*

Approximately 85 species of *Nicrophorus* are described, 20 of which are found in the New World and 15 of these are found north of Mexico (Peck & Anderson 1985). Ecological aspects of six old world and 11 new world *Nicrophorus* species have been investigated (Pukowski 1933, Anderson & Peck 1985, Kozol et al. 1988, Scott & Traniello 1990, Robertson 1992, Trumbo 1994 and citations therein), but the bionomics of western and southern Nearctic species remains poorly known. All the well-studied *Nicrophorus* species occur in regions that experience harsh winters and the biology of species from environments lacking harsh winters, such as the central coast of California, is poorly understood.

*Nicrophorus* biology, particularly reproductive behavior, is well described (Pukowski 1933, Trumbo 1994, and citations therein). In brief, interspecific and intrasexual competition occur for dominance of small (< 100 g) carcasses. Carcasses dominated by *Nicrophorus* adults are buried by a male–female pair and used as a food resource for developing offspring. The larvae develop within a brood chamber which also houses the parents and the carcass. Both parents tend the larvae by regurgitating food, maintaining the brood chamber and defending the brood against predators or competing congeners. Numerous aspects of burying beetle behavior, such as biparental care, communal breeding, brood parasitism,

[1] Present Address: Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269.

etc. have been recently explored from a behavioral ecology perspective (Bartlett 1988; Bartlett & Ashworth 1988; Müller et al. 1990; Scott 1990; Trumbo 1990a, 1991, 1994; Trumbo & Wilson 1993; Trumbo & Fiore 1994; Eggert & Müller 1992; Scott & Gladstein 1993).

*Nicrophorus nigrita* Mannerheim, occurs along the Pacific coast, from British Columbia to Baja California and inland to Nevada, (Anderson & Peck 1985, Peck & Anderson 1985). It is the most common silphid in California (Miller & Peck 1979). These large, black beetles are present in most Californian ecosystems, yet current knowledge is limited to data gathered from museum specimens.

The lack of dorsal, elytral maculations on *N. nigrita* adults is a species-level trait unique among Nearctic *Nicrophorus.* Anderson & Peck (1986) suggest a thermoregulatory hypothesis, supported by the evidence that melanic morphs of *Nicrophorus guttula* Motschulsky, *Nicrophorus defodiens* Mannerheim and *Nicrophorus investigator* Zetterstedt are found in regions of reduced levels of solar radiation, where *N. nigrita* is common. If *N. nigrita* is adapted to environmental conditions unique for Nearctic burying beetles, as suggested by its dark coloration, then other traits associated with this adaptation should exist. This investigation, in addition to providing new natural history information, attempts to test this prediction.

I investigated the hypothesis that *N. nigrita* displays additional traits associated with its lack of elytral maculations, and documented this species' life history. During 1991 and 1992, I collected information on abundance, phenology, sex ratio, morphology, diel periodicity, population size, carrion community species composition, habitat preference and reproductive biology from a central Californian, coastal population of *N. nigrita.*

## Materials and Methods

*Study Site.*—Research was conducted from 19 Apr 1991 to 7 Mar 1992 at the University of California Landels-Hill Big Creek Reserve. The reserve is located within the Santa Lucia coastal mountain range, Monterey County, California (36°4′ N, 121°36′ W). The topography is convoluted with mountain ridges reaching elevations above 600 m. Extreme climatic variation and steep elevational gradients in the reserve are associated with many diverse communities. Twelve plant communities exist within the reserve, with redwood (*Sequoia sempervirens* (D. Don) Endlicher), oak (*Quercus* spp.), bay (*Umbellularia californica* (Hooker & Arnott) Nuttall), and coastal sage scrub (*Artemisia* spp., *Baccharis* sp., *Ceanothus* sp. et al.) being members of the more common communities (Bickford & Rich 1985).

*Live Trapping.*—Traps were positioned throughout the reserve to sample beetle abundance over time and to obtain sex ratio and body size data. Eight 1 $m^2$ hanging live-catch pitfall traps (Wilson et al. 1984), were modified by adding a funnel inside the collecting entrance, fashioned from a 12 oz. plastic Solo (R) cup minus its bottom, to prevent beetles from escaping. Traps were opened on 19 Apr 1991 and were rebaited at ten day intervals with 250 g of rotten chicken that had been contained for 2–5 days at ambient temperature. Starting in mid October, traps were rebaited at monthly intervals and trapping ceased 7 Mar 1992.

Population abundance and phenology were evaluated by recording trap catches at ten day intervals and by marking, releasing and recapturing beetles. Captured

*N. nigrita* were marked by cutting a triangular piece, approximately 1 $mm^2$ in size, from the posterior margin of an elytron (Wilson & Knollenberg 1987, Trumbo 1990b, Goldwasser et al. 1993) before releasing them at the trap site. I also obtained phenology information from museum specimens of the California Academy of Sciences Entomology Collection in San Francisco and the Entomology Collection of the University of California at Davis.

Sex ratio and morphology were evaluated by sexing trapped individuals and by measuring their pronotal widths (to 0.05 mm). Sex determinations were based on this species' sexual dimorphism: the male's foretarsi are wider and have more pubescence than the female's and the male has larger ridges above the eyes and a larger clypeus than the female. Dried beetles obtained from the traps were weighed to evaluate the relationship between pronotal width and mass (Bartlett & Ashworth 1988, Scott 1990, Robertson 1992).

Diel periodicity was investigated by using a single trap located in a redwood-forested canyon bottom, that was checked once for beetles an hour before and once an hour after sun-up and sun-set. The data represent thirty days of observations, spanning 16 Jul to 30 Aug 1991.

Insect specimens of species not previously seen in the hanging traps were collected and identified (Table 3). Only presence/absence data were recorded for species other than *N. nigrita.* Voucher specimens of these species were deposited in the Montana Entomology Collection, Montana State University. A long series of adult *N. nigrita* specimens was deposited in the research collection at the Landels-Hill Big Creek Reserve.

A minimum population size for this species within Big Creek Canyon (one of four canyons sampled) was estimated using a sequential, Bayesian algorithm (Gazey & Staley 1986, Kozol et al. 1988). To help meet assumptions of the algorithm, data from a single trap run from 22 May to 21 Oct 1991 in Big Creek Canyon were used.

*Mouse Carcass Transect Studies.*—Habitat preference was assessed by monitoring mouse carcass transects. Dead laboratory mice, (*Mus musculus* L.), thawed 10–15 h before use and weighing 15–35 g, were spaced on transects at 20 m intervals in seven habitats (Table 4). Each mouse was attached to a flag marker by 0.5 m of copper wire that prevented their removal by invertebrates, yet allowed burial by beetles and subsequent carcass location. The mice were observed daily for the first three days and every other day thereafter. I eventually recorded all mice as being dominated, displaced or consumed. During these observations, I hand collected representatives of the Coleoptera and Hymenoptera found on the mouse carcasses (Table 3). Voucher specimens of these species were deposited in the Montana Entomology Collection, Montana State University.

*Laboratory Reproduction Studies.*—Wild pairs of beetles obtained from hanging traps were placed with freshly thawed mouse carcasses in plastic 2 liter reproduction chambers (RC). Each RC had a perforated lid, was filled with soil from a redwood-forested, canyon-bottom floor and contained one pair of beetles and a mouse carcass. The RCs were kept in a well aerated room within the reserve, where the photoperiod and temperature fluctuated with external conditions. Laboratory temperatures ranged from 13 to 20 °C. To test for seasonal reproductive activity, wild-caught adults were placed in RCs on the following dates: 3 May, 5 Jul, 28 Jul, 24 Sep and 5 Nov 1991.

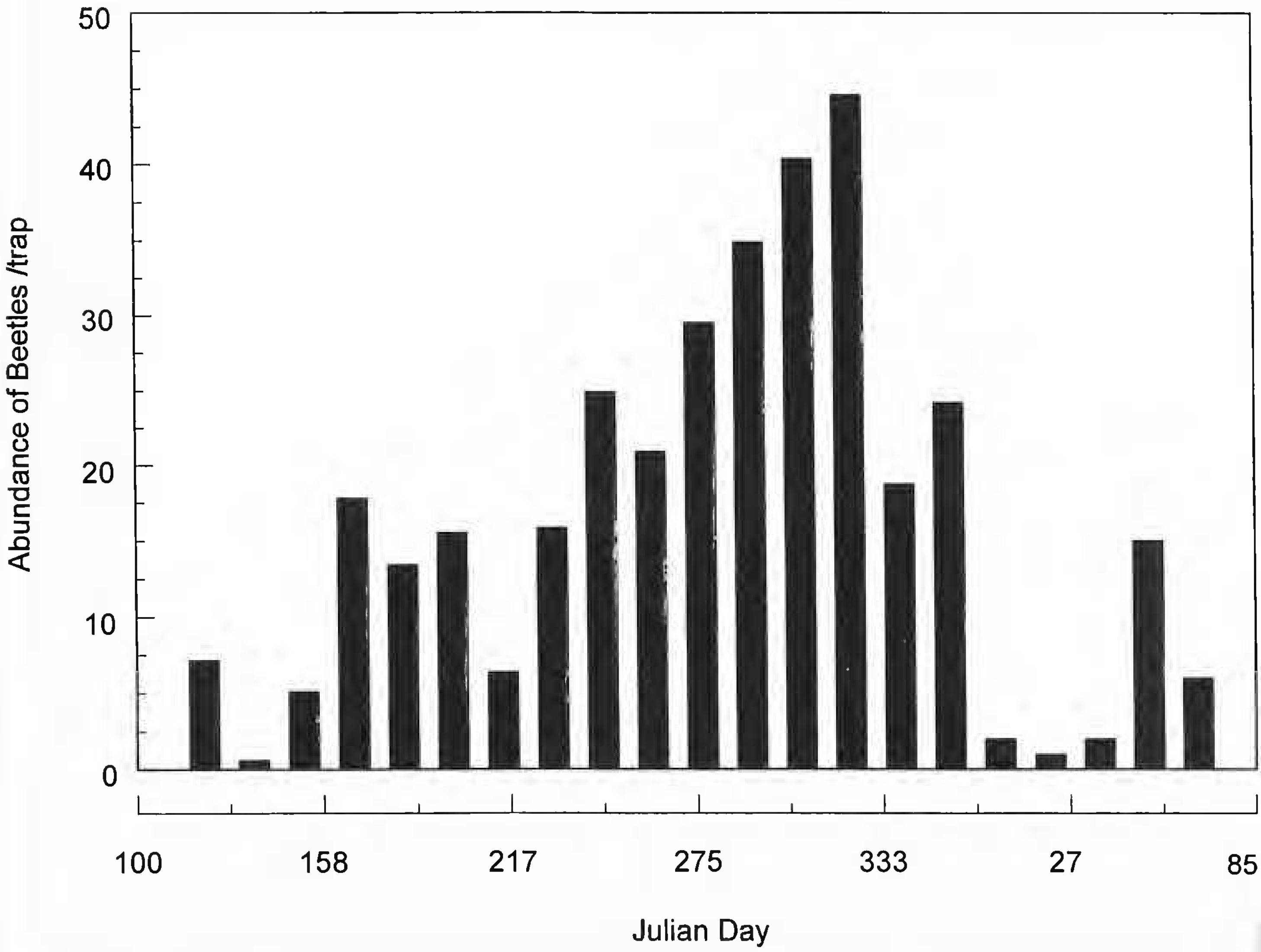


Figure 1. Abundance of adult *Nicrophorus nigrita* captured in hanging pitfall traps; day 120 (1991) = first trap capture = (30 Apr 1991); day 67 (1992) = last trap capture = (7 Mar 1992).

Quantitative data on the duration of parental care, duration of larval feeding and the number of emerging progeny were obtained by observing activity within the RCs daily. Fecundity data were obtained by counting the number of larvae per brood on day 12. Sex ratios and pronotal widths of the emerging adults from 40 RCs were recorded.

Other aspects of *Nicrophorus* reproductive biology, such as the creation of a brood ball and biparental care, were noted during the course of the study, but no quantitative data were gathered. Phoretic mites were collected and identified for comparative purposes. Mite specimens were deposited in the private collection of B. M. O'Connor.

*Reproductive Success.*—I investigated the following three variables as possible predictors of reproductive success: paternal pronotal width, maternal pronotal width and mouse carcass size. Reproductive success was measured by two variables: the number of offspring, and the mean pronotal width of the offspring in a brood. I also determined the relationship between offspring size and days from burial to eclosion.

## Results

*Live-trapping.*—The abundance of *N. nigrita* adults steadily increased throughout the summer but decreased sharply with the onset of cooler weather and greater precipitation in early November (Fig. 1). However, *N. nigrita* adults were captured

Table 1. Pronotal width of *Nicrophorus nigrita* (mm) captured in hanging-pitfall traps.

| Sex | $n$ | Mean (SD) | Min. | Median | Max. | Var. |
|---|---|---|---|---|---|---|
| ♂ | 862 | 5.84 (0.74) | 3.90 | 5.85[a] | 7.85 | 0.55 |
| ♀ | 1022 | 5.67 (0.66) | 3.70 | 5.70[a] | 7.52 | 0.44 |

[a] Males significantly larger than females, Mann-Whitney test, H = 24.27, df = 1, $P = 0.000001$.

throughout the winter. Specimens of *N. nigrita* in the California Academy of Sciences Entomology Collection and the UC Davis Entomology Collection had been collected during each month of the year ($n = 611$). In 313 days of trapping, 2349 *N. nigrita* adults were caught. I marked and released 1497 *N. nigrita* adults, of which 123 (8.2%), were later recaptured.

The sampled, wild population of *N. nigrita* had a female-biased sex ratio (0.84: 1.0, $n = 1884$; differs significantly from 1:1 $\chi^2 = 13.58$, df = 1, $P < 0.05$). The combined $F_1$ sex ratio of 32 laboratory reared broods was male-biased (1.08:1.0, $n = 354$; differs significantly from 1:1 $\chi^2 = 7.59$, df = 1, $P < 0.05$).

The mean pronotal width of males was greater than that of females (Table 1). Pronotal width was found to be a positive predictor of dried beetle mass ($n = 214$, linear correlation $r = 0.65$, $P < 0.001$, Kendall's Tau = 0.461, $P = 1.47 \times 10^{-23}$).

*Nicrophorus nigrita* adults were most often caught at dusk, with some catches recorded at dawn and fewer recorded during the night (Table 2). No beetles were caught during the day (Table 2).

The agyrtid, *Necrophilus hydrophiloides* Guérin-Méneville, was commonly captured in the hanging pitfall traps during the winter months when silphids were rare (Table 3).

Within Big Creek Canyon a total of 623 beetles were marked during 23 capture-mark-release events and 83 (13%) were recaptured. I calculated a minimum population size of 4565 beetles (95% confidence intervals of 1832 and 5866 individuals).

*Mouse Carcass Transect Studies.*—Fifty-eight of 90 dead mice placed on transects were displaced by vertebrate scavengers (64%). Two transects placed over 100 m from a trail or road were the least disturbed by vertebrates (Table 4). Table 3 lists Coleoptera and Hymenoptera species found associated with mouse carcasses.

Table 2. Diel Periodicity of *Nicrophorus nigrita* adults caught in a hanging pitfall trap.

| Time intervals | | # Days | Total hrs. obs[a] | # Beetles observed[b] |
|---|---|---|---|---|
| Daytime | >06:30 h <20:00 h | 6 | 81 | 0 |
| PM crepuscular | >20:00 h <21:00 h | 8 | 8 | 18 |
| Night | >21:00 h <05:30 h | 10 | 85 | 5[c] |
| AM crepuscular | >05:30 h <06:30 h | 6 | 6 | 3 |

[a] Total hrs. obs. is the total number of hours during the specified time intervals that were sampled for beetle presence.

[b] Beetles were most often caught at sundown ($\bar{x}^2 = 405.4$, df = 3, $P < 0.0001$).

[c] Four beetles trapped on a cloudless night of full moon, 29 Aug 1991.

Table 3. Coleoptera and Hymenoptera species caught in hanging pitfall traps baited with 280 g rotten chicken, and on mouse carcasses in a variety of habitats (see Table 4), May through Oct 1991.

| Order, family | Species | Mouse carcasses | Traps |
|---|---|---|---|
| COLEOPTERA | | | |
| Silphidae | *Nicrophorus nigrita* Mannerheim | X | X |
| | *Nicrophorus guttula* Motschulsky | | X |
| Agyrtidae | *Necrophilus hydrophiloides* Guérin-Méneville | | X |
| Staphylinidae | *Creophilus maxillosus* (L.) | | X |
| Dermestidae | *Dermestes marmoratus* Say | X | X |
| | *Dermestes talpinus* Mannerheim | | X |
| | *Megatoma* sp. | | X |
| Leiodidae | *Catops simplex* Say | | X |
| Histeridae | *Saprinus* prob. *lugens* Erichson | | X |
| Melyridae | *Collops* sp. | X | |
| Cleridae | *Necrobia rufipes* (De Geer) | | X |
| HYMENOPTERA | | | |
| Vespidae | *Vespula vulgaris* (L.) | X | |
| Braconidae | *Alysia* nr. *alticola* (Ashmead) | X | |
| Formicidae | *Solenopsis xyloni* McCook | X | |
| | *Solenopsis molesta* (Say) | X | |
| | *Crematogaster* (*mormonum* Emery or *coarctata* Mayr) | X | |
| | *Monomorium ergatogyna* Wheeler | X | |
| | *Formica moki* Wheeler | X | |
| | *Camponotus* nr. *vicinus* Mayr | X | |

*Nicrophorus nigrita* only buried mice in cool, mesic, redwood habitats (Table 4). Temperature fluctuations within these habitats were less severe than habitats found near or on ridge tops (unpubl. weather station data).

*Laboratory Reproductive Studies.*—Wild *N. nigrita* adults were reproductively active in the laboratory from 3 May to 5 Nov 1991. The means of the number of offspring produced from three independent rearing attempts were 15.6 (SD = 11.7, $n$ = 3 broods), 15.3 (SD = 6, $n$ = 8 broods) and 12.6 (SD = 5.6, $n$ = 40 broods). Male parents remained with the brood for a mean of 11.1 days (SD = 1.2, $n$ = 6 broods) whereas females remained with the brood for a mean of 13.1 days (SD = 2.3, $n$ = 7 broods). Paternal residence time was not significantly shorter than maternal ($t = -1.98$, df = 9.5, $P = 0.076$). Together, parents tended offspring for a mean of 10.9 days (SD = 1.5, $n$ = 8 broods).

Larvae began pupation a mean of 12.3 days (SD = 1.2, $n$ = 3 broods) after the adults had been placed with a dead mouse (initiated 3 May 1991). Approximately 80 days elapsed between placement of adults with a dead mouse and the emergence of offspring from their pupal chambers (mean = 79.9, SD = 6.6, $n$ = 10 broods, initiated 28 Jul 1991).

Features of *N. nigrita* biology consistent with other known *Nicrophorus* spp. include: construction of a brood chamber and a brood "ball"; deposition of anal compounds onto the carcass purported to inhibit growth of bacteria and fungi (Pukowski 1933, Halffter et al. 1983); departure of the male parent prior to the female parent; regurgitation of food to the larvae by the parents; stridulation by the parents while tending the young; three instars of larval development; and the

Table 4. The proportion of mouse carcasses displaced, dominated or consumed by vertebrates or saprophagous arthropods in 10 locations, over 10 days, Aug and Sep 1991.

| Habitat | Approx. elevation | *n* | *N. nigrita* | Vertebrates | Flies | Ants | *Vespula vulgaris* | Other |
|---|---|---|---|---|---|---|---|---|
| rwd[a]/mesic W sl[b] | 90 m | 10 | 0.10 | 0.10[c] | 0.80 | | | |
| rwd/mesic N sl | 90 m | 10 | 0.10 | 0.90 | | | | |
| rwd/mesic N sl | 90 m | 10 | | 0.90 | 0.10 | | | |
| rwd/mesic N sl | 90 m | 5 | | 1.00 | | | | |
| rwd/mesic N sl | 150 m | 11 | 0.40 | [c] | 0.60 | | | |
| rwd/xeric S sl | 90 m | 10 | | 0.70 | 0.10 | 0.20[d] | | |
| grass/xeric hltp | 300 m | 10 | | 0.40 | | 0.40[e] | | 0.20 |
| oak/xeric hltp[f] | 480 m | 5 | | 1.00 | | | | |
| *Pinus*/xeric S sl | 678 m | 9 | | 0.89 | | | 0.11 | |
| coast scrub N sl | 330 m | 10 | | 1.00 | | | | |
| | | mean %: | 6 | 69 | 16 | 6 | 1 | 2 |

[a] rwd = redwood.
[b] sl = slope.
[c] Transect laid >100 m from trail or road.
[d] *Solenopsis xyloni.*
[e] *Solenopsis molesta.*
[f] hltp = hilltop.

presence of phoretic mites and nematodes. The nematodes occasionally bred to enormous population levels on carcasses in the laboratory causing the beetles to abandon the carcasses—a previously unreported competitive interaction.

Three species of phoretic mites taken from *N. nigrita* adults were identified as *Poecilochirus carabi* Canestrini (Parasitidae), *Poecilochirus subterraneus* (Mueller) (Parasitidae) and *Pelzneria* sp. (Histiostomatidae). These mites were all removed from adult beetles and were deutonymphs.

*Reproductive Success.*—No adult offspring were produced by 8 (20%) of 40 RCs begun on 28 Jul 1991. Within the 32 remaining broods, a total of 465 larvae were counted on day 12 after initiation. In the predator-free, laboratory environment, 354 (76%) of these larvae survived to eclosion. A significant, positive relationship was found between days to eclosion and pronotal width of emerging adults ($n$ = 354, $r^2 = 0.17$, $P < 0.01$).

Mouse carcass mass predicted the pronotal widths of emerging adults but paternal and maternal size did not. Mouse carcass mass (using mouse tissue parcels weighing 2.75–42 g) was significantly related to mean pronotal width of the offspring in a brood ($n$ = 37 broods, $r^2 = 0.419$, $P < 0.0001$; Fig. 2). Carcass mass was a weak positive predictor of the number of larvae found on day 12 ($n$ = 37 broods, $r^2 = 0.104$, $P = 0.052$) but not a predictor of the number of emerging adult offspring ($n$ = 37 broods, $r^2 = 0.0039$, $P = 0.71$).

## Discussion

*Live-trapping & Mouse Carcass Transect Studies.*—The phenologies of *N. nigrita* and its hypothesized sister species, *Nicrophorus mexicanus* Matthews (Peck & Anderson 1985), are unique among the documented phenologies of Nearctic *Nicrophorus* because adults of these species remain active in low numbers during

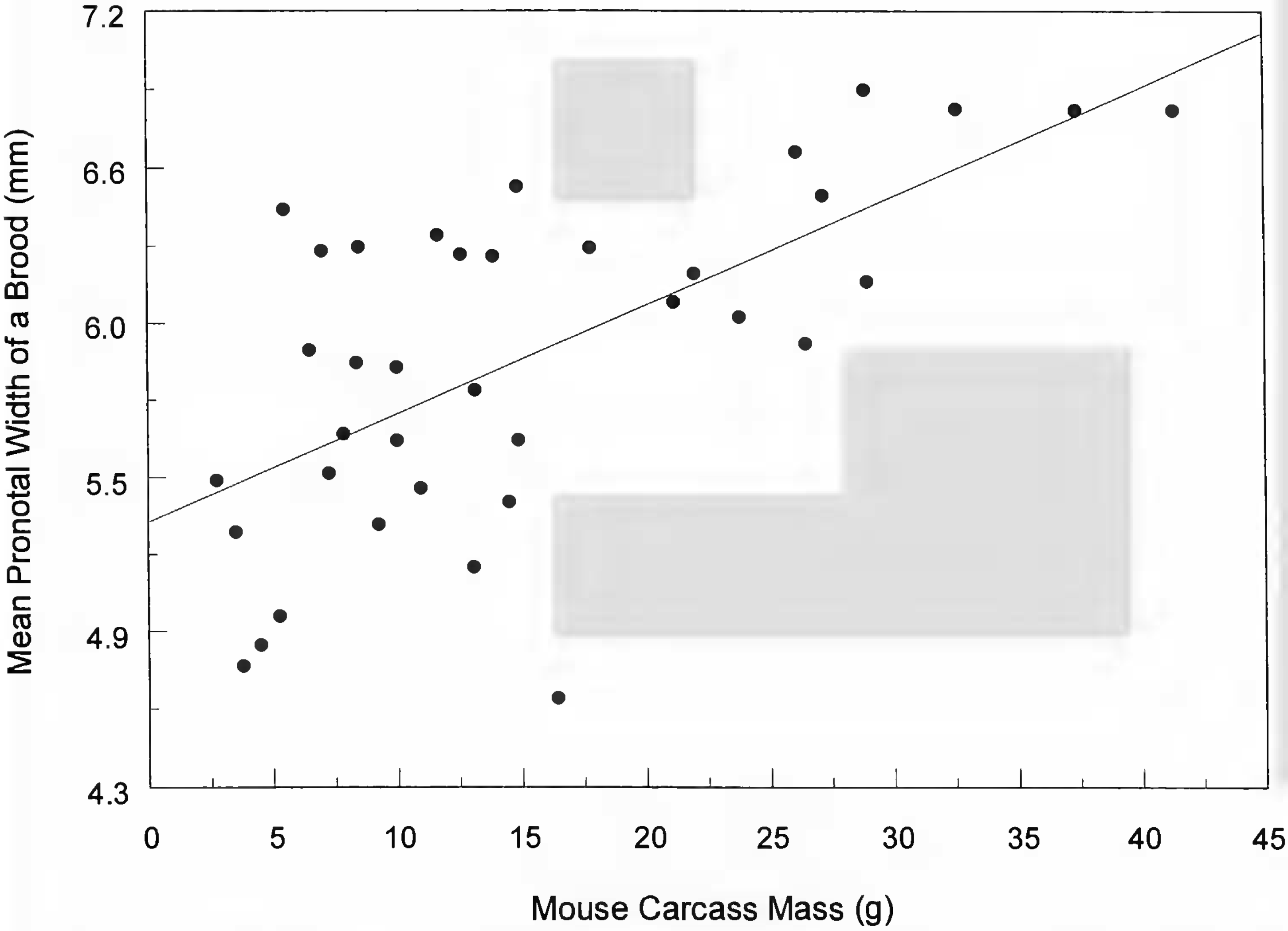


Figure 2. Relationship between mouse carcass mass and the mean pronotal width of the offspring in a brood for *Nicrophorus nigrita,* ($n$ = 37 broods, Kendall's Tau = 0.42, $P$ = 0.000265; linear correlation: $r$ = 0.648, $P < 0.001$, pronotal width = 0.0407 (carcass mass) ± 5.29).

winter months (Terron et al. 1991). These two species are found in regions that generally lack cold winters, a factor related to their year-round activity. Species in the southern United States, such as *Nicrophorus carolinus* Linnaeus, may also remain active during the winter months due to the mild winters of those regions.

Peck & Anderson (1985) and Anderson & Peck (1985) state that *N. mexicanus* and *N. nigrita* adults are most active during fall, winter and spring—a finding not corroborated by this investigation. Terron et al. (1991) document *N. mexicanus* as being most active during the summer, and least active during the winter, which is consistent with my observations of *N. nigrita.*

Terron et al. (1991), studying *N. mexicanus,* Trumbo (1990a), studying *Nicrophorus orbicollis* Say and Wilson & Knollenberg (1984), studying *N. orbicollis* and *N. defodiens* found female-biased sex ratios at pitfall traps. Trumbo (1990a) found 1:1 sex ratios for *Nicrophorus pustulatus* Herschel and *Nicrophorus tomemtosus* Weber, whereas male-biased sex ratios were found in Palearctic *Nicrophorus* spp. studied by Easton (1979) and Springett (1967). Wilson & Knollenberg (1984) and Trumbo (1990a) both reported laboratory raised broods were non-biased suggesting intrinsic and/or extrinsic factors skew the sex ratios in *N. mexicanus, N. orbicollis, N. tomentosus* and *N. nigrita.*

This study indicates *N. nigrita* adults are crepuscular (Table 2), whereas *N. nigrita* had been reported to be a nocturnal species based on data from black light captures (Peck & Kaulbars 1987). The method used here, provides data more representative of natural behavior than black-light data (Wilson et al. 1984). However, I recorded activity during a brightly moon-lit night (Table 2), suggesting these beetles may prolong their period of activity under such conditions.

*Nicrophorus defodiens* is active crepuscularly in Michigan (Wilson et al. 1984), whereas *N. tomentosus* is diurnal and two other species, *N. orbicollis* and *Nicrophorus sayi* LaPorte, were documented to be strictly nocturnal. My data support the nocturnal and crepuscular activity pattern more commonly found in this genus.

The low proportion of transect mouse carcasses dominated by *N. nigrita* adults (Table 4) may result from a number of causes. Vertebrate scavengers, most likely foxes, consumed the majority of dead mice placed in the field. Similar results, with vertebrate scavengers removing from 60% to 100% of small carcasses, are not uncommon (Putman 1976, 1983). *Nicrophorus nigrita* adults were more successful in using carrion in areas where vertebrate scavengers have less impact as seen in the two transects located more than 100 m from a trail or road (Table 4). Other arthropod species may outcompete *N. nigrita* for carrion within the study region (Table 3). It is unclear whether *N. nigrita* prefers to breed on large carcasses, as some congeners have been shown to do (e.g. *N. pustulatus*; Peck 1986, Robertson 1992, Trumbo & Wilson 1993). If shown to occur, this would help explain the scarcity of adults on small carcasses in the field.

*Laboratory Reproductive Studies.*—The reproductive biology of *N. nigrita* is similar to other *Nicrophorus.* The greatest difference found, in addition to the apparent lack of reproductive diapause, involved the time required to complete development. Robertson (1992) reports that Canadian *N. pustulatus* complete development from larva to adult in 22–27 d. Scott & Traniello (1990) report *N. orbicollis* from New Hampshire require approximately 44 d from burial of a carcass to eclosion. Halffter et al. (1983), studying *N. mexicanus,* found development was completed from larva to adult in 39 days. These records are significantly shorter than the corresponding 73–85 d development time required for *N. nigrita.* However, these traits may be population-level adaptations, or simple plastic (non-fixed) responses to the temperature of the environments or laboratories in which the species were studied, rather than fixed, species-level traits. Robertson (1992), Scott & Traniello (1990), and Halffter et al. (1983) did not state at what temperature the larvae developed, but all three of these studies were conducted within laboratories, which generally range from 15 to 25° C.

The reproductive phenologies of many Nearctic *Nicrophorus* are known (Wilson et al. 1984, Scott & Traniello 1990, Anderson & Peck 1985). *Nicrophorus nigrita* displays a less constrained reproductive schedule than those of congeners that are tightly associated with the seasonal changes present in the eastern and northern Nearctic. *Nicrophorus nigrita* females are able to reproduce within a month of eclosion (unpublished data) and no evidence of reproductive diapause was found, although reproduction in the field during the months of December to April has yet to be demonstrated.

The reproductive success of *N. nigrita* is consistent with that of other congeners. *Nicrophorus orbicollis* shows no correlation between female size and offspring number (Scott & Traniello 1990), but does show a strong correlation between carcass size and total brood mass (Scott & Traniello 1990, Robertson 1992, Trumbo 1994). I found similar relationships for *N. nigrita.*

Scott & Traniello (1990) found a significant negative correlation between brood size and days to eclosion for *N. orbicollis.* This is consistent with my findings showing offspring size to be positively correlated with days to eclosion; brood size and offspring size have been shown to be inversely related (Scott & Traniello 1990).

The departure of the male parent prior to the female has been reported from other *Nicrophorus* (Bartlett 1988; Müller & Eggert 1989; Scott 1990; Scott & Traniello 1990; Trumbo 1991). I did not establish that male *N. nigrita* adults abandon their offspring prior to females, however, this is most likely a result of small sample sizes rather than strong evidence against the pattern of early male departure. Scott & Gladstein (1993) present a predictive model and analysis of the sociobiological ramifications of the duration of paternal care in burying beetles.

The geographic and phylogenetic distance (Peck & Anderson 1985) between *N. nigrita* and the more well-known eastern species predicted differences were likely to be found in the phoretic mite fauna of *N. nigrita.* Of the three mite species found on *N. nigrita, P. carabi* is Holarctically distributed and the most commonly reported phoretic associate of *Nicrophorus* spp. (Brown & Wilson 1992). *Poecilochirus subterraneus* is not documented to occur in the Nearctic but is widespread in the Palearctic (B. M. O'Connor, personal communication). There are no described Nearctic species within the genus *Pelzneria* (B. M. O'Connor, personal communication). The presence of a Palearctic species of phoretic mite (*P. subterraneus*) on *N. nigrita* indicates a possible biogeographic Asian connection. The diversity and complexity of the phoretic fauna found on *Nicrophorus* spp. has attracted attention (Wilson 1983, Wilson & Knollenberg 1987, Schwarz & Müller 1992, Richter 1993) but many avenues of ecological and systematic research remain open (Brown & Wilson 1992).

In conclusion, I suggest that the autapomorphic aspects of *N. nigrita*'s biology are associated with this species' thermoregulatory adaptation to survival in regions of cool but relatively constant temperatures. This hypothesis was first proposed by Anderson & Peck (1986) for the melanic forms of *N. guttula, N. investigator* and *N. defodiens* found predominantly along the pacific coast. The autapomorphic aspects of *N. nigrita* are the continual activity throughout the winter months (possible synapomorphy with *N. mexicanus*), the prolonged time span to complete development from larva to adult, the apparent lack of seasonally-fixed reproductive activity and the absence of bright elytral maculations. Future studies investigating behavioral and ecological correlates of *Nicrophorus* thermoregulation are needed to test this hypothesis.

## Acknowledgment

I am grateful to J. T. Smiley for providing advice, supplies and help throughout this study. I thank M. E. Sikes for her assistance in the field and encouragement, D. S. Wilson, S. T. Trumbo and S. B. Peck for sharing information regarding *Nicrophorus,* the collection managers N. Penny (CAS) and S. Heydon (UCDC) for their assistance, reviewers R. S. Miller, M. A. Ivie, J. T. Smiley, D. K. Letourneau, C. Seibert, and two anonymous reviewers whose input improved the manuscript, P. Ward (Formicidae), S. Heydon (Braconidae), D. Carmean (Vespidae), B. O'Connor (Acari) and M. A. Ivie (Coleoptera) for their identifications and S. V. and A. Sikes and F. Arias for their technical support. Financial support was provided by F. F. Bliss, J. T. Smiley, S. V. and S. B. Sikes and The Department of Biology, University of California, Santa Cruz. This research was carried out as part of a Senior Thesis in Biology at UCSC. This is contribution J-3007 of the Montana Agricultural Experiment Station.

## Literature Cited

Anderson, R. S. & S. B. Peck. 1985. The insects and arachnids of Canada, Part 13: the carrion beetles of Canada and Alaska (Coleoptera: Silphidae & Agyrtidae). Canadian Government Publishing Centre, Ottawa. 121 pp.

Anderson, R. S. & S. B. Peck. 1986. Geographic patterns of colour variation in North American *Nicrophorus* burying beetles (Coleoptera; Silphidae). J. Nat. Hist., 20: 283–297.

Bartlett, J. 1988. Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav. Ecol. Sociobiol., 23: 297–303.

Bartlett, J. & C. M. Ashworth. 1988. Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav. Ecol. Sociobiol., 22: 429–434.

Bickford, C. & P. Rich. 1985. Vegetation and flora of the Landels-Hill Big Creek Reserve, Monterey County, California. (2nd ed.). UCSC Environmental Field Program Publication No. 15, 122 pp.

Brown, J. M. & D. S. Wilson. 1992. Local specialization of phoretic mites on sympatric carrion beetle hosts. Ecology 73: 463–478.

Easton, C. 1979. The ecology of burying beetles. Ph.D. Dissertation, University of Glasgow, Glasgow, Scotland.

Eggert, A-K. & J. K. Müller. 1992. Joint breeding in female burying beetles. Behav. Ecol. Sociobiol., 31: 237–242.

Gazey, W. J. & M. J. Staley. 1986. Population estimation from mark-recapture experiments using a sequential Bayes algorithm. Ecology, 67: 941–951.

Goldwasser, L., G. E. Schatz & H. J. Young. 1993. A new method for marking Scarabaeidae and other Coleoptera. Coleopt. Bull., 47: 21–26.

Halffter, G. S., S. Anduaga & C. Huerta. 1983. Nidification des *Nicrophorus.* Bull. Soc. Entomol. Fr., 88: 648–666.

Kozol A. J., M. P. Scott & J. F. A. Traniello. 1988. The American burying beetle, *Nicrophorus americanus:* studies on the natural history of a declining species. Psyche, 95: 167–176.

Miller, S. E. & S. B. Peck. 1979. Fossil carrion beetles of Pleistocene California asphalt deposits, with a synopsis of Holocene California Silphidae (Insecta: Coleoptera: Silphidae). Trans. San Diego Soc. Nat. Hist., 19: 85–106.

Müller, J. K. & A-K. Eggert. 1989. Paternity assurance by "helpful" males: adaptations to sperm competition in burying beetles. Behav. Ecol. Sociobiol., 24: 245–249.

Müller, J. K., A-K. Eggert & J. Dressel. 1990. Intraspecific brood parasitism in the burying beetle, *Necrophorus vespilloides* (Coleoptera: Silphidae). Anim. Behav., 40: 491–499.

Peck, S. B. & R. S. Anderson. 1985. Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). Quaest. Entomol., 21: 247–317.

Peck, S. B. 1986. *Nicrophorus* (Silphidae) can use large carcasses for reproduction (Coleoptera). Coleop. Bull., 40: 44.

Peck, S. B. & M. M. Kaulbars. 1987. A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. Proc. Entomol. Soc. Ont., 118: 47–81.

Pukowski, E. 1933. Ökologische untersuchungen an *Necrophorus* F. Zeitschr. Morphol. Öekol. Tiere, 27: 518–586.

Putman, R. J. 1976. Energetics of the decomposition of animal carrion. Ph.D. Dissertation, Oxford University.

Putman, R. J. 1983. Carrion and dung: the decomposition of animal wastes. Stud. biol. No. 156. Edward Arnold, London. 62 pp.

Richter, S. 1993. Phoretic association between the dauerjuveniles of *Rhabditis stammeri* (Rhabditidae) and life history stages of the burying beetle *Nicrophorus vespilloides* (Coleoptera: Silphidae). Nematologica 39: 346–355.

Robertson, I. C. 1992. Relative abundance of *Nicrophorus pustulatus* (Coleoptera: Silphidae) in a burying beetle community, with notes on its reproductive behavior. Psyche, 99: 189–198.

Scharwz, H. H. & J. K. Müller. 1992. The dispersal behaviour of the phoretic mite *Poecilochirus carabi* (Mesostigmata, Parasitidae): adaptation to the breeding biology of its carrier *Necrophorus vespilloides* (Coleoptera, Silphidae). Oecologia, 89: 487–493.

Scott, M. P. 1990. Brood guarding and the evolution of male parental care in burying beetles. Behav. Ecol. Sociobiol., 26: 31–39.

Scott, M. P. & J. F. A. Traniello. 1990. Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). Anim. Behav., 39: 274–283.

Scott, M. P. & D. S. Gladstein. 1993. Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. Evol. Ecol., 7: 362–378.

Springett, B. P. 1967. The biology of *Necrophorus* (Col.) and the mortality of terns (Sterna); an ecological study. Ph.D. Dissertation, University of Durham, Durham, England.

Terron, R. A., S. Anduaga & M. A. Moron. 1991. Analisis de la coleopterofauna necrofila de la reserva de la biosfera "La Michilia", Durango, Mexico. Folia Entomol. Mex., 81: 315–324.

Trumbo, S. T. 1990a. Reproductive success, phenology and biogeography of burying beetles (Silphidae: *Nicrophorus*). Am. Midl. Nat., 124: 1–11.

Trumbo, S. T. 1990b. Interference competition among burying beetles (Silphidae: *Nicrophorus*). Ecol. Entomol., 15: 347–355.

Trumbo, S. T. 1991. Reproductive benefits and the duration of paternal care in a biparental burying beetle, *Necrophorus orbicollis*. Behaviour, 117: 82–105.

Trumbo, S. T. & D. S. Wilson. 1993. Brood discrimination, nest mate discrimination, and determinants of social behavior in facultatively quasisocial beetles (*Nicrophorus* spp.). Behav. Ecol., 4: 332–339.

Trumbo, S. T. & A. J. Fiore. 1994. Interspecific competition and the evolution of communal breeding in burying beetles. Am. Midl. Nat., 131: 169–174.

Trumbo, S. T. 1994. Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. Oikos, 69: 241–249.

Wilson, D. S. 1983. The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. Am. Nat., 121: 851–870.

Wilson, D. S. & W. G. Knollenberg. 1984. Food discrimination and ovarian development in burying beetles (Coleoptera: Silphidae: *Nicrophorus*). Ann. Entomol. Soc. Am., 77: 165–170.

Wilson, D. S., W. G. Knollenberg & J. Fudge. 1984. Species packing and temperature dependent competition among burying beetles (Silphidae: *Nicrophorus*). Ecol. Entomol., 9: 205–216.

Wilson, D. S. & W. G. Knollenberg. 1987. Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. Evol. Ecol., 1: 139–159.